Social transmission of lichenivory feeding tradition in captive Yunnan snub-nosed monkeys: foraging decisions, adaptive radiation and conservation implications

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Abstract

The peculiar feeding habit of lichenivory shown by *Rhinopithecus* species has allowed them to adapt to high altitude alpine environments. Such remarkable ecological radiation is known only in this primate genus, three of whose species are living at the highest altitudes known for primates. Nevertheless, not much is known of how this behavior is acquired and transmitted. By observing how captive *Rhinopithecus* individuals not used to lichenivory acquire this feeding skill, we can infer how this same behavior could have been instilled in the wild in evolution. Here, we report on observations made in the Beijing Zoological Gardens, in China, where all Yunnan snub-nosed monkeys (*R. bieti*) have acquired lichenivory. From 2013, this habit was gradually transmitted socially from a wild captured alpha male to all group members. Our finding shows that co-feeding and social facilitation are elements involved in the acceptance of novel food intake, going through initial stages of adaptation by overcoming neophobia. The lichenivory acquisition process which we report brings evidence that this behavior was learned culturally by new generations. We finally discuss the conservation implications for the rehabilitation and reintroduction project of snub-nosed monkeys and other primates in the wild.

Key worlds: *Rhinopithecus bieti*; novel food; social facilitation; cultural transmission; conservation.

Introduction

Social learning is a process that allows the inheritance and transmission of behaviors that become part of the culture of the individuals that display them (Castro and Toro 2004; e.g. Leca et al. 2007; Jaeggi et al. 2010). Especially in primates, we know that this skill can shape foraging decisions (Rapaport and Brown, 2008; van de Waal et al. 2013) and advance the adaptation of a species to local environments (Rendell et al. 2010). Naive individuals can include novel food types into their dietary spectrum and avoid the risk of poisoning, as long as the food consumed by the knowledgeable individuals had the same physical characteristics as the novel food acquired by the naive individuals (Visalberghi and Addessi 2001; Vale et al. 2017). The experienced individuals can become skill-acquisition models for their own offspring and neighboring companions. New feeding habits established in a population can ease environmental pressures, affecting genetic and phenotypic evolution leading to adaptive radiation and ultimately speciation (Thornton and Clutton-Brock 2011; Dukas 2013; Tran 2014).

Overcoming neophobia for novel food and the formation of new feeding habits through social facilitation have been found in lemurs (Gosset and Roeder 2001; O'Mara and Hickey 2012), New World monkeys (Addessi and Visalberghi 2001; Visalberghi et al. 2003; Yamamoto and Lopes 2004; Galloway et al. 2005; Voelk et al. 2006), Old World monkeys (Cambefort 1981; Tarnaud and Yamagiwa 2008; Laidre 2009); and great apes (Huffman et al 2010; Finestone et al. 2014; Gustafsson et al. 2014; Hardus et al. 2015; Gustafsson et al. 2016). No studies to date have however reported novel food acquisition by social learning and social facilitation in colobines. Snub-nosed monkeys belong to the genus *Rhinopithecus,* one of the Asian colobines, comprising five species: Sichuan snub-nosed monkey, *R. roxellana*; Yunnan snub-nosed monkey, *R. bieti*; Myanmar snub-nosed monkey, *R. strykeri*; Guizhou snub-nosed monkey, *R. brelichi*;

and Tonkin snub-nosed monkey *R. avunculus*. They live in multilevel societies across varied environments, from limestone rain forests to alpine mountains, and exhibit vast dietary flexibility, from frugivory to folivory to lichenivory (Kirkpatrick and Grueter 2010). Feeding on lichens is rarely found in mammals but appears unique to three of the snub-nosed monkeys (*R. roxellana, R. bieti,* and *R. strykeri)*, Barbary macaques (*Macaca sylvanus*), and Norwegian reindeer (*Rangifer tarandus*) as a fallback strategy for overwintering in harsh environments (Guo et al. 2007; Ménard 2002; Storeheier et al. 2002; Grueter et al. 2009; Yin Yang, unpublished data). In this paper, we report for the first time events of lichenivory acquired and transmitted in captive *R. bieti* individuals at the Beijing Zoological Gardens through social learning. We then discuss the significance of this event in relation to social facilitation and adaptive radiation of the species of *Rhinopithecus*, and novel implications for primate conservation.

Methods

The Beijing Zoological Gardens (BZG) started to keep their first *R. bieti* in 1994. The subject was a male juvenile captured from Baima Snow Mountains National Nature Reserve in 1989 (see Tab. 1). During the past 13 years, *R. bieti* in BZG have been breeding to the third generation through introduction and exchanges of new individuals. Currently, there are three captive *R. bieti* units in BZG, including two units with three individuals each and one unit with five individuals. The three units are separated and housed in indoor–outdoor enclosures and are fed in the outdoor parts (indoor enclosure: 32.4 m^2 and 3.5 m high; outdoor enclosure: 146.3 m^2 and 12.7 m high). The enclosures are equipped with perches, rockery and play facilities. All enclosures are separated by tempered glasses and the families can watch each other through these glass windows. Fresh fruits, leaves and vegetables are used to provision the monkeys.

Since 2013 and every following year, one bag (11 kg) of dry lichen (*Usnea longissima*) has been purchased and shipped from the area of Baima Snow Mountains for feeding the captive *R. bieti* with the purpose of increasing the diversity of their feeding regime. The amount of lichens can be used continuously to feed all *R. bieti* in BZG for a month. The keepers documented which individuals ate lichens and the approximate daily quantity. In this report, we review and analyze these records. For reconstructing the events, we also sent a number of questionnaires to the keepers and elaborated on the results.

The observations

We here report on the observations recorded from 2013 from three monkey units housed in BZG and one in Kunming Zoo (KMZ) in Yunnan province. These observations and the increasing feeding rate on the novel food are summarized in Figure 1.

In August 2013, when the keepers first served the lichens to Unit 1, Nandi, the oldest monkey in his all-male unit (see individuals' information in Table 1), immediately came to grab and eat in considerable amount. Daqing and Dingding were resident with Nandi. Daqing also took the initiative to have a share of the lichens, by taking some in his hands, but he quickly dropped them without eating them. The second day, Daqing kept on picking the lichens and keeping an eye on Nandi's eating behavior. Finally, on the third day, he tasted the lichens. A third monkey, Dingding, the youngest individual of the unit, also showed both neophobia and later neophilia for the new food. A keeper described Dingding's behavior similar to "the one of an infant accidentally catching a caterpillar" when he obtained this food for the first time. "He screamed while throwing the lichens around". After repeating this behavior several times in the next few days and seeing that Nandi was eating a considerable amount of this food, Dingding tasted the lichens and chewed them up. He seemed not to really feed on them, however, since he did not keep chewing and only swallowed a small amount. Conversely, he played with the rest as with a toy. The following year, Dingding followed Nandi and did eat the lichens, nevertheless maintaining some hesitation. After the third year, Dingding gave the impression of appreciating the lichens much more, stealing some of Nandi's share of lichens when not noticed by this more dominant individual. It therefore took much longer for Dingding, compared to Daqing, to totally like this new food type.

Still in August 2013, in the second, adjacent unit, the male named Agui also started to eat the lichens after observing that the keepers were serving the lichens to Nandi (Figure 1: Photo A). This happened after the third day. In the following days, Agui was followed by Huahua, his breeding female, and eventually also by their male baby, Chuangchuang. In the second year, this unit ate the lichens without any hesitation. The newborns Xiaowu and Yaomei, male and female respectively, were both recorded to spontaneously feed on lichens at the age of 10 months. Yaomei liked to seize lichens from her mother's hand to eat. It should be noted that the captive newborns at BZG feed independently in their 10^{th}-11^{th} month of age. Infants initially acquire non-breastfed food from their mother's hand and mouth, and Xiaowu and Yaomei, began to feed on lichens right at the onset of their weaning.

The third monkey unit consists of the male Daqing, his breeding female Anan, and their female baby Fangfang. These individuals had been resident in Shisanling breeding base since 2014. The female Anan was transferred from the Kunming Institute of Zoology of the Chinese Academy of Science (KIZ-CAS). This individual was used to feeding on lichens, since this food was given customarily to all *R. bieti* at KIZ-CAS. When the Shisanling keepers first served lichens to this family, as expected, the habituated Anan ate without hesitation, while Daqing took Fangfang's discards and ate them showing some indecision. With time, after seeing Anan and Daqing eating the lichens on multiple instances, Fangfang began to eat the new food. By 2015, the lichens had become popular foods for all three units. Since then, the keepers had to separate and distribute the lichens to every individual to avoid the alpha males monopolizing most given of them.

The last observations we report were taken from the separately housed male named Xiaobeijing (Figure 1: Photo B). He was born in 1999 at BZG, and later transferred to KMZ in 2003. In 2016, the keepers attempted to offer lichens to Xiaobeijing; he handled them from the first, but never took up the habit of feeding on them, despite the fact that the keepers kept on scattering this food in the enclosure at successive attempts. As a singly housed male, this monkey never showed lichenivory.

We should add that lichens were also used to provision *R. brelichi* at BZG and *R. roxellana* at BZG and KMZ. Only a male of *R. roxellana*, Zhuangzhuang, tried to taste the lichens once, while the other individuals at BZG showed some handling behavior only. When the keepers gave lichens to *R. brelichi*, they showed some evident neophobia or at least disinterest, since none of them was ever noticed to touch them. Similarly, a couple of *R. roxellana* at KMZ only came to look the lichens over but were never noticed to acquire them for feeding (Figure 1: Photo C).

Discussion

Since being taken from his natural habitat, 24 years ago, the *R. bieti* male named Nandi has kept on being a lichen consumer, allowing for the initiation of this behavior in his captive group. This long time span provides us with an indication that wild-caught individuals can maintain their feeding habits outside of their natural environment, as long as that specific food is provided to them. The case we have described offers new evidence on how lichenivory is instilled in a colobine group: the new habit is transmitted from experienced to naïve individuals by means of co-feeding and social facilitation. One individual, Xiaobeijing, was never able to adjust to lichenivory, despite the attempts of the keepers at providing him with this food type. We put this down to the fact that he was kept in isolation from the other individuals; he was therefore not exposed to visual stimuli, did not go through the learning process from an experienced individual, and never enhanced this behavior.

Compared with other subadults (Daqing, Dingding and Chuangchuang), the juveniles (Yaomei and Xiaowu) showed a long-lasting feeding behavior typical of natural lichen-eaters - an indication that not only there are age-dependent effects in relation to social foraging (Schiel and Huber 2006), but also that co-feeding accelerates the transmission of these behavioral innovations (Coussi-Korbel and Fragaszy 1995; van de Waal et al. 2013; Hardus et al. 2015). Once these behaviors are consistently shown by the group members, they shape the feeding habits of the offspring allowing for a survival advantage after weaning (Tarnaud 2004; Ueno 2005; O'Mara and Hickey 2012). The accelerated lichenivory-acquisition rate shown by these *R. bieti* units suggests that lichenivory in *Rhinopithecus* is culturally transmitted (see Lefebvre 1995). In our case, we observed lichenivory to be accelerated by mother-infant transmission (van de Waal et al. 2014).

It is important to notice that different *Rhinopithecus* species may evolve different cultural traditions of lichen preference in the wild due to the different floristic composition of the varied habitats occupied. Although *Usnea longissima* can be found in the habitat of *R. roxellana*, *R. bieti*, and *R. brelichi*, it has in fact been reported that *R. roxellana* mostly feeds on the lichen *Ramalina sinensis* which is prevalent in the deciduous tree forests of the Qingling Mountains (Guo et al. 2007). *R. bieti*, instead, mainly feeds on the lichens of *Bryoria spp.* in its northern distributional range, but more frequently on *Usnea longissima* in its southern distribution among the conifers of the Yunling Mountains (Kirkpatrick 1996; Grueter et al. 2009). *Rhinopithecus roxellana* in the mixed evergreen and deciduous forests of Qingmuchuan in the Qingling Mountains (Li et al. 2010), *R. brelichi* of the subtropical evergreen broadleaved forests of the Fanjing Mountains (Xiang et al. 2012), and *R. avunculus* of the limestone tropical rain forests in Vietnam (Quyet et al. 2007) are not used to lichenivory because other abundant and more nutritious food resources are available year around. We can lastly speculate that lichenivory acquired by an ancestral *Rhinopithecus* population enabled them to adapt to the rapid uplift of the Himalayan region and to overcome the Last Glacial Maximum of the middle and late Pleistocene era. Due to this event, the snub-nosed monkeys radiated into the present alpine environment while speciating in succession into *R. roxellana, R. bieti* and *R. strykeri* (Zhou et al. 2016).

Our findings can also be analyzed in view of conservation projects for the rehabilitation and the reintroduction of *Rhinopithecus* and other primates. The Kunming Institute of Zoology is intending to rehabilitate their captive reared *R. bieti* and reintroduce them into an area in the historic range (Lü Longbao, pers. comm.); experience from other projects, however, has shown how the release of captive reared primates has very often been accompanied by high mortality rates in the initial stages of the post release period - imbalance of food provision, failing to distinguish fallback foods, and lack of information of high-quality foraging locations for the releases are all elements being pointed to as detrimental to the survival of reintroduced primates (Stoinski et al. 2003; Peignot et al. 2008; Russon et al. 2009; Millán et al. 2014). Under natural conditions, the *Rhinopithecus* diet is habitat specific. The different species have been able to adapt their feeding habits following phenological changes (Guo et al. 2007; Grueter et al. 2009; Li et al., 2010; Xiang et al. 2012), climate changes (Li et al. 2003), and habitat alterations (Guo et al. 2008). Our finding suggests that, due to long-term artificial feeding, the released individuals will most likely suffer from high mortality because of not being experienced at feeding on the primary food or fallback resources of their new habitat. In case the rehabilitated monkeys cannot return to their birthplace, we recommend before reintroduction to investigate (1) the food types available in the intended release area, (2) whether the area holds enough edible resources and (3) which varied candidate food sources, especially currently primary and fallback foods, should be presented to the rehabilitating individuals to get accustomed to when still in captivity;

thus (4) presenting wild-caught experienced individuals in the rehabilitating group can promote customization process of wild food and group level of foraging knowledge. By doing so, the reintroduced individuals will have a higher chance of survival in the wild.

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Conflict of interest

The authors declare that they have no conflict of interest.

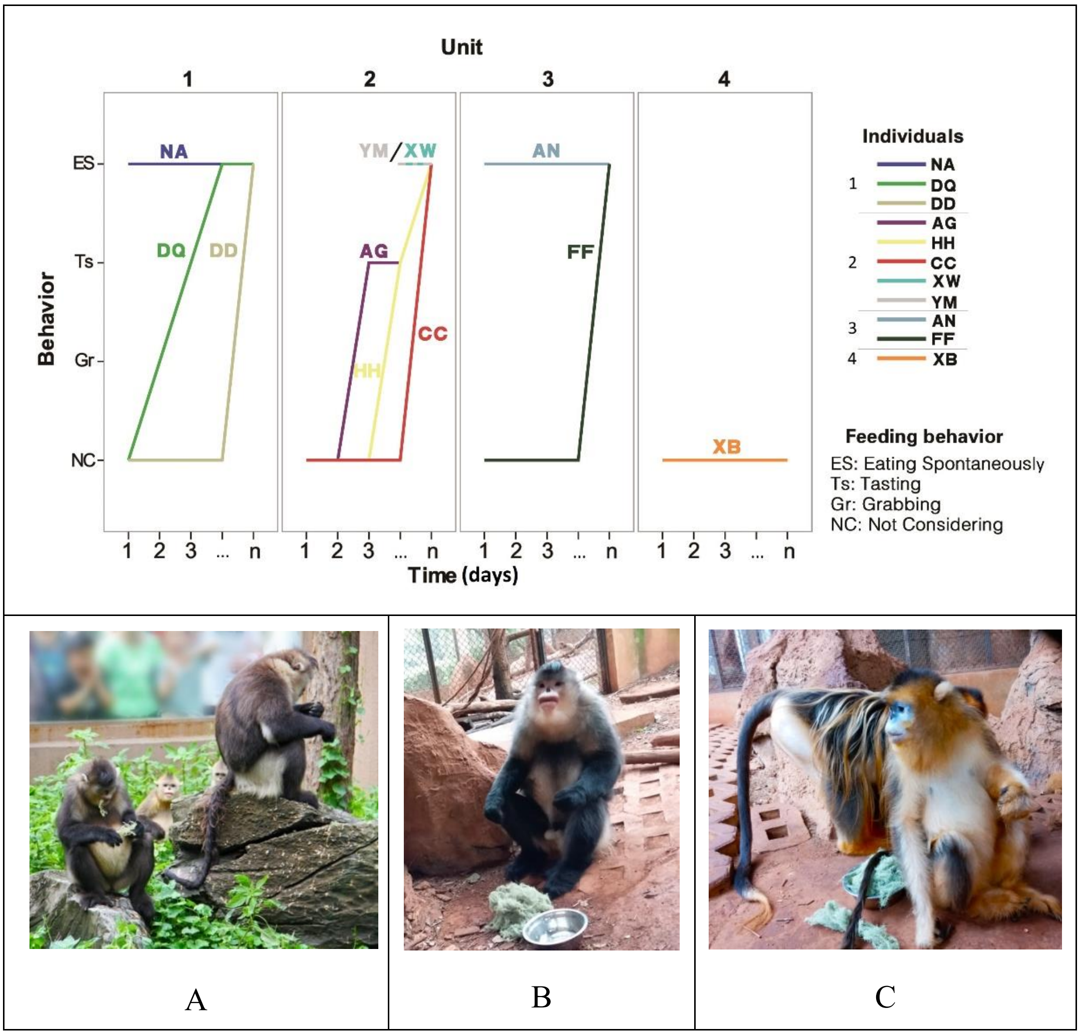

Figure 1. Top graph: behavioral trend of the *Rhinopithecus bieti* individuals observed feeding on lichens of *Usnea longissima* according to time and monkey unit. As long as an initiator can be observed in the unit, the other individuals will gradually feed on the lichens. Photo A: the individuals Agui and Huahua from Unit 2 are feeding on lichens while the juveniles Yaomei and Xiaowu wait for their turn and observe the adults' feeding behaviour at Beijing Zoological Garden; Photo B: although being offered the appropriate species of lichens, the singly housed XiaoBeijing does not show any interest in them at Kunming Zoo; Photo C: even when presented to them, a couple of *Rhinopithecus roxellana* in Kunming Zoo does not feed on this species of lichens.

Table 1. Yunnan Snub-nosed Monkey (*Rhinopithecus bieti*) Studbook

Stud#	Unit	Name	Sex	Birth Day	Sire	Dam	Location	Date — Event
15	1	Nandi	M	~/Apr/1989	Wild	Wild	BSM KMZ BZG	~/Apr/1989 — Capture ~/Apr/1989 — Transfer 8/Apr/1994 — Transfer
19	2	Yuanyuan	F	27/Jan/1991	7	8	KMZ BZG BZG	27/Jan/1991— Birth 8/Apr/1994 — Transfer 22/Aug/2009 — Death
26	3	Anan	M	11/Apr/1997	2	13	KIZ-CAS KMZ BZG	11/Apr/1997 — Birth 27/Sep/2000 — Transfer 17/Oct/2012 — Loan to
30	4	Xiaobeijing	M	13/Feb/1999	15	19	BZG KMZ	13/Feb/1999 — Birth 13/Nov/2003 — Transfer
33	2	Agui	M	31/May/1999	UNK	14	KMZ BZG	31/May/1999 — Birth 09/Nov/2003 — Transfer
36	2	Huahua	F	18/Mar/2001	15	19	BZG	18/Mar/2001 — Birth
45	3	Fangfang	F	09/Apr/2007	33	36	BZG	09/Apr/2007 — Birth
N	1	Daqing	F	21/Mar/2009	33	36	BZG	21/Mar/2009 — Birth
N	1	Dingding	F	22/Feb/2011	33	36	BZG	22/Feb/2011 — Birth
N	2	Chuangchuang	M	12/May/2012	33	36	BZG	22/Feb/2011 — Birth
N	2	Xiaowu	M	11/May/2014	33	36	BZG	11/May/2014 — Birth
N	2	Yaomei	F	24/Mar/2016	33	36	BZG	24/Mar/2016 — Birth

Note: N = None; UNK = Unknown; M = Male; F = Female; BSM = Bama Snow Mountains; KIZ-CAS = Kunming Institute of Zoology, Chinese Academy of Sciences; KMZ = Kunming Zoo; BZG = Beijing Zoological Gardens.